

Comparison of growth traits between abundant and uncommon forms of a non-native vine, *Dolichandra unguis-cati* (Bignoniaceae) in Australia

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Abstract

Cat's claw creeper vine, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) (Bignoniaceae), is a major environmental weed in Australia. Two distinct forms of this weed ('long' and 'short' pod), with differences in leaf morphology and fruit size, occur in Australia. The long pod form has only been reported in less than fifteen localities in the whole of south-east Queensland, while the short pod form is widely distributed in Queensland and New South Wales. This study sought to compare growth traits such as specific leaf area, relative growth rate, stem length, shoot/root ratio, tuber biomass and branching architecture between these forms. These traits were monitored under glasshouse conditions over a period of 18 months. Short pod exhibited higher values of relative growth rates, stem length, number of tubers and specific leaf area than long pod, but only after 10 months of plant growth. Prior to this, long and short pod did not differ significantly. Higher values for these traits have been described as characteristics of successful colonizers. Results from this study could partly explain why the short pod form is more widely distributed in Australia while long pod is confined to a few localities.

Keywords

Cat's claw creeper, invasive species, competitiveness, relative growth rate, successful colonizers, traits, biomass, tubers

Introduction

Invasive plant species continue to threaten biodiversity and ecosystem function globally (Heckel 2004; Pimentel et al. 2005). A fundamental objective of invasion ecology is to identify a suite of plant traits that may determine invasion success in novel environments (Pyšek and Richardson 2007; Richardson and Pyšek 2006; van Kleunen et al. 2010). An outcome of this search can be traced back to Baker's ideal weed hypothesis, in which Baker (1965) proposed a set of plant traits most likely to be exhibited by invasive species. Comparative studies between exotic invasive species and their native non-invasive congeners have contributed immensely to our understanding of traits that promote colonisation and invasion success by some species (e.g. van Kleunen et al. 2011).

It has proven difficult to consistently find a correlation of the same set of traits with invasiveness, likely because of the varying effects of environmental factors on different plant species (Alpert et al. 2000; Burns 2006). Studies have shown that no particular trait solely confers invasiveness on a species, rather it is how a species responds to different environmental conditions that contributes to its fitness and abundance (Firn et al. 2012; Leishman et al. 2010; Osunkoya et al. 2010; Pattison et al. 1998). Plastic responses of invasive plants to varying environmental conditions increase their competitiveness and fitness (Claridge and Franklin 2002). Therefore, multiple factors likely explain the success of invasive plant species (Blumenthal 2005; Daehler 2003; Lamarque et al. 2011; Leffler et al. 2014; Leung et al. 2004; MacDougall et al. 2009). For example, Burns (2006) found that invasive species had higher specific leaf area (SLA) and relative growth rates (RGR), but only under certain environmental conditions. Nevertheless, a pattern of relatedness to invasiveness has been reported for some plant traits (Pyšek and Richardson 2007). Mostly, traits that have direct relatedness to plant physiological performance such as leaf area ratio, growth rate, shoot/root allocation and propagule pressure show marked differences between evidently invasive and non-invasive species (Grotkopp et al. 2002; van Kleunen et al. 2010).

Invasive species were shown to have higher values of traits like SLA (Burns 2006; Lake and Leishman 2004), RGR (Dawson et al. 2011), and more biomass allocated to organs like stems, resulting in taller plants (Gallagher et al. 2015; Stanisci et al. 2010; van Kleunen et al. 2015). High SLA is often associated with high RGR (Grotkopp and Rejmánek 2007), although other studies have not found that trend (see, for example, Garcia-Serrano et al. 2005). Overall, fast growing plants have generally been found to be more likely to be invasive than others (Blumenthal and Hufbauer 2007; Lake and Leishman 2004; Richardson 1998). Higher values for these traits in invasive species compared to less invasive ones imply different strategies for capturing and using resources such as light, carbon, nitrogen and moisture (Gallagher et al. 2015). Because resources are almost always limiting in the environment (Cordell et al. 1998), efficient use of limiting resources by invasive species can enhance their colonizing success (Pattison et al. 1998). In disturbed environments, species that are better able to exploit fluctuating resources will likely invade the system (Cordell et al. 1998; Leffler et al. 2014; van Kleunen et al. 2010).

Most studies aimed at understanding differences in traits associated with invasion success have used native species as control plants (Muth and Pigliucci 2006). The limitation of this approach is that these native species may already be invasive elsewhere (van Kleunen et al. 2010). For example, some native species used in a comparative study by Godoy et al. (2011) were reported to be invasive in other parts of the world. Other studies have also shown that these traits do not always differ between invasive and non-invasive species (Meiners 2007; Smith and Knapp 2001; Thompson et al. 1995). An assessment of 122 species including non-native invasive and native species that occupy disturbed areas did not find significant differences in these traits (Leishman et al. 2010). Muth and Pigliucci (2006) argue that some native species were shown to have invasive tendencies in their native range, implying that introduced vs native species comparisons may not always be informative (but see Blossey and Notzold 1995; Callaway and Ridenour 2004; Dawson et al. 2015; Keane and Crawley 2002; van Kleunen et al. 2011). There could also be a bias in choosing highly competitive invasive species and comparing them with known weak native competitors in pairwise experiments (Vila and Weiner 2004) or comparing phylogenetically non-related species (Burns 2006).

Our understanding of invasiveness traits could be better enhanced by comparing related non-native species of varying levels of colonization success (Kolar and Lodge 2001; Muth and Pigliucci 2006; van Kleunen et al. 2010). In this study, we compare different traits between two forms of an invasive vine, cat's claw creeper, that appear to have significantly different levels of invasion success. Cat's claw creeper, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) was introduced as an ornamental into Australia from South America in the 1800s (Dhileepan 2012; Downey and Turnbull 2007; Gentry 1976). *D. unguis-cati* is now a declared environmental weed and considered formally as a Weed of National Significance (WoNS) in Australia (Thorp and Lynch 2000).

Dolichandra unguis-cati prefers forested and riparian habitats, although it also grows vigorously on dry road side sunny environments. It also appears to thrive in most soil types, tolerating a wide range of soil pH (Downey and Turnbull 2007). Two forms of this species with distinct leaf morphology occur in Australia (Dhileepan 2012; Shortus and Dhileepan 2011). The two forms of *D. unguis-cati* were named long pod (LP) and short pod (SP) due to differences in their average fruit (pod) length at maturity (LP: 700.2 ± 23.5 mm; SP: 300.9 ± 89.6 mm) (Shortus and Dhileepan 2011). While LP occurs in isolated localities of south-east Queensland (Qld), SP occurs extensively in Qld and New South Wales, often in dense infestations (Dhileepan 2012; Downey and Turnbull 2007). These two forms appear to prefer similar habitats, although there is general lack of research on the ecology of this species (Osunkoya et al. 2009). The LP and SP forms have been shown to carry an average of 120 ± 10 and 60 ± 23 seeds per pod at maturity, respectively (Shortus and Dhileepan 2011). Seeds of both forms are two-winged, papery and flattened/oblong in shape, 10–18 mm long, 4.2–5.8 mm wide. The average seed biomass is not significantly different between the forms of *D. unguis-cati* (mean seed biomass for LP: 16.60 ± 0.65 mg and for SP: 15.65 ± 0.83 mg)

(Shortus and Dhileepan 2011). Previous studies have found that the two forms showed differences in some life history traits. Boyne et al. (2013) found a wide variety of leaf morphology for this species, but also reported that SP had significantly more simple leaves than LP.

In a field experiment using plants generated from tubers, Taylor and Dhileepan (2012) found that LP produced greater total dry mass (hence higher RGR) than SP although the study did not measure such parameters as specific leaf area (SLA) and leaf area ratio (LAR). SP was shown to have rapid and higher germination rates than LP at varying temperature regimes (Buru et al. 2014). SP was also reported to exhibit significantly higher frequencies of polyembryony than LP, at times one seed producing quadruplet seedlings (Buru et al. 2016). The only study on the seed bank ecology of the most prevalent form (SP) by Vivian-Smith and Panetta (2004), found it to have low seed longevity, usually less than 12 and 1% at 1 year for soil-surface (< 1 cm depth) and 5 cm depth buried seeds, respectively. Osunkoya et al. (2009) also noted some differences in stem density of genets and ramets between the two forms in field samples, but decried lack of data on growth rates and reproductive capacity for the two forms.

Herbarium records and field surveys suggest that LP is widely distributed in the native range, occurring from Mexico, Nicaragua, Costa Rica, Columbia to Brazil, whereas SP appear to be restricted to Paraguay (Dhileepan 2012; K. Dhileepan, personal observations). In Australia, previous field surveys have revealed that there were seven sites in south-east Queensland (Qld) where LP has been reported, two at which it co-occurs with SP (Boyne et al. 2013; Dhileepan 2012; Shortus and Dhileepan 2011). Recently, seven more sites were identified, bringing the total number of known sites to 14 in south-east Qld where LP occurs (Liz Snow (Biosecurity Queensland), pers. comm. 7/03/2016).

The cause for the observed differences in abundance levels between LP and SP is not yet established, but introduction pressure may be one explanation. Reconstructing the invasion history of this exotic species (or the two forms) is not possible because there are no records of their introduction, except that the species was first reported in a Melbourne Nursery catalogue in 1865 (Downey and Turnbull 2007). Introduction history of most ornamental plants is generally not or poorly recorded (Harris et al. 2007; Prentis et al. 2009). Studies on whether there has been any deliberate breeding selection of the species that resulted in the two forms are yet to be done.

Another explanation could be differences in growth strategies between LP and SP. Rapid growth and efficient resource allocation enhance success in colonization, especially during the early stages of plant life history (Bachmann et al. 2012; Luo et al. 2015). Considering that LP and SP show marked abundance differences in Australia, comparing important functional traits of the two forms may assist with understanding whether different growth strategies explain the different populations. Significantly higher values of growth related traits for one form could infer different strategies of resource use (Dawson et al. 2011; Godoy et al. 2011). Here we sought to compare traits such as SLA, RGR, stem length, shoot/root ratio, tuber biomass and branching

architecture between the two forms of *D. unguis-cati* plants grown from seeds. We did this to develop a type of prospectus on the growing strategies of the two forms of *D. unguis-cati* that may begin to explain differences in their distributions and abundance.

Methods

Experimental design

In 2013 seeds of LP and SP were collected from various sites around the greater Brisbane area in southeast Queensland, Australia. Sites were chosen based on accessibility and availability of mature seeds at the time of experimentation. Once collected, seeds were stored for two weeks at room temperature in paper envelopes that were placed in containers with silica gel to ensure they were dry before germination commenced. Seeds were sterilised by soaking in 1% sodium hypochlorite (NaOCl) for 5 minutes followed by rinsing in water for 3 minutes (Mijani et al. 2013). Seed germination dynamics of the two forms carried out in growth chambers were discussed in detail in Buru et al. (2016).

After two weeks of germination, seedlings were transferred into plastic pots (dimensions: Width = 200 mm, Height = 190 mm, Length = 200 mm) filled with locally available commercial multi-purpose potting mix (Osmocote) containing a professional wetting agent and trace elements. This seedling growth experiment was set up at the Ecosciences Precinct glasshouse facilities (GPS coordinates: 27°29'41.5248"S; 153°1'49.2132"E) in Brisbane, Australia. The average temperature during the warmer months (October – April) ranged from 18 °C to 35 °C while during the cooler months (May – September) it was between 10 °C and 23 °C. Relative humidity ranged between 50 – 60% during this study. Plants were watered once a day but no additional fertilizer/nutrients were added. For this experiment, plants were left to grow without any support. Seedlings were left to grow in a light environment (range: 60–250 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$) over 18 months (October 2013–March 2015), with sub-samples of plants taken at 5 and 10 months. Seven seedlings (replicates) were used per form (LP and SP) at each observation time. These replicates were randomly selected from an initial pool of over 100 plants raised from seeds. The remaining plants were used for other eco-physiological studies.

At observation time, vernier callipers were used to measure basal stem diameter (BSD) at the root-stem junction. Leaf area was determined by taking leaf pictures against a graduated background using a Panasonic DMC-ZS7, Lumix camera and then using the open access software Image J 1.47v (www.imagej.nih.gov/ij) to calculate the leaf area in cm^2 . Two mature leaves (including petiole) per replicate were used for this purpose. Fresh and dry masses of these leaves were also determined.

For each replicate plant, stem length, number of primary branches and ramifications (secondary branches), number of tubers and tuber fresh weight were also recorded. Apical dominance index (ADI) was calculated by dividing the number of ramifications

by the total length of the branch in metres according to Pérez-Harguindeguy et al. (2013). At each harvest period, whole plants were separated into above- and below-ground parts. Shoots, roots and tubers were separated and then dried in an oven at 80 °C for 72 hours (Cornelissen et al. 2003). Dry weights were measured using an electronic analytical model AUW120D, Mettler Toledo digital scale. Root, shoot and tuber dry weights were divided by the total dry weight to determine root, shoot and tuber mass ratio respectively (Garcia-Serrano et al. 2005). RGR was estimated by absolute change in total dry weight, above- and below-ground tissue dry weight, tuber dry weight and stem length between the 10th and 18th month divided by the number of months (see Taylor and Dhileepan 2012). Other resultant parameters such as specific leaf area (SLA) and leaf dry matter content (LDMC) or leaf matter per area (LMA) were calculated following Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013).

Statistical analysis

Differences in RGR and other traits such as SLA, LDMC, total dry mass, belowground/aboveground biomass ratio, number of tubers, tuber mass ratio (TMR), shoot mass ratio (SMR) and root mass ratio (RMR) were compared using two-way MANOVA model, with form and age of plant as independent variables. Interactions of form and age of plants were also included in the model. When significant differences were found, a Tukey LSD post-hoc test was performed to check differences between specific means. Differences or similarities in plant traits between LP and SP were further analysed using a Principal Component Analysis (PCA). The clusters were projected on the graphical representation of the first two PCA axes. All statistical tests were conducted using R version 3.1.0 (R Development Core Team 2014). PCA was performed using an add-on *vegan* package (version 2.3-4) in R (Dixon 2003).

Results

Biomass production and allocation

The overall total dry mass differed significantly between the two forms after 18 months of plant growth ($F_{1,36} = 73.802, p < 0.001$). There was a significant interaction between form and age of the plant on the total dry mass ($F_{2,36} = 6.371, p < 0.004$). During the earlier stages of growth up to 10 months, there was no significant difference between the two forms in terms of total dry mass accumulation, although generally SP weighed more (Table 1 and Fig. 1a).

Above- and below-ground biomass allocation (also shown by shoot/root ratio) did not vary significantly between forms ($F_{1,39} = 2.568, p > 0.08$), and no significant interactions of form and age of plant were detected on this trait. A Tukey test of multiple comparisons of means showed that the proportion of dry biomass allocated to shoots,

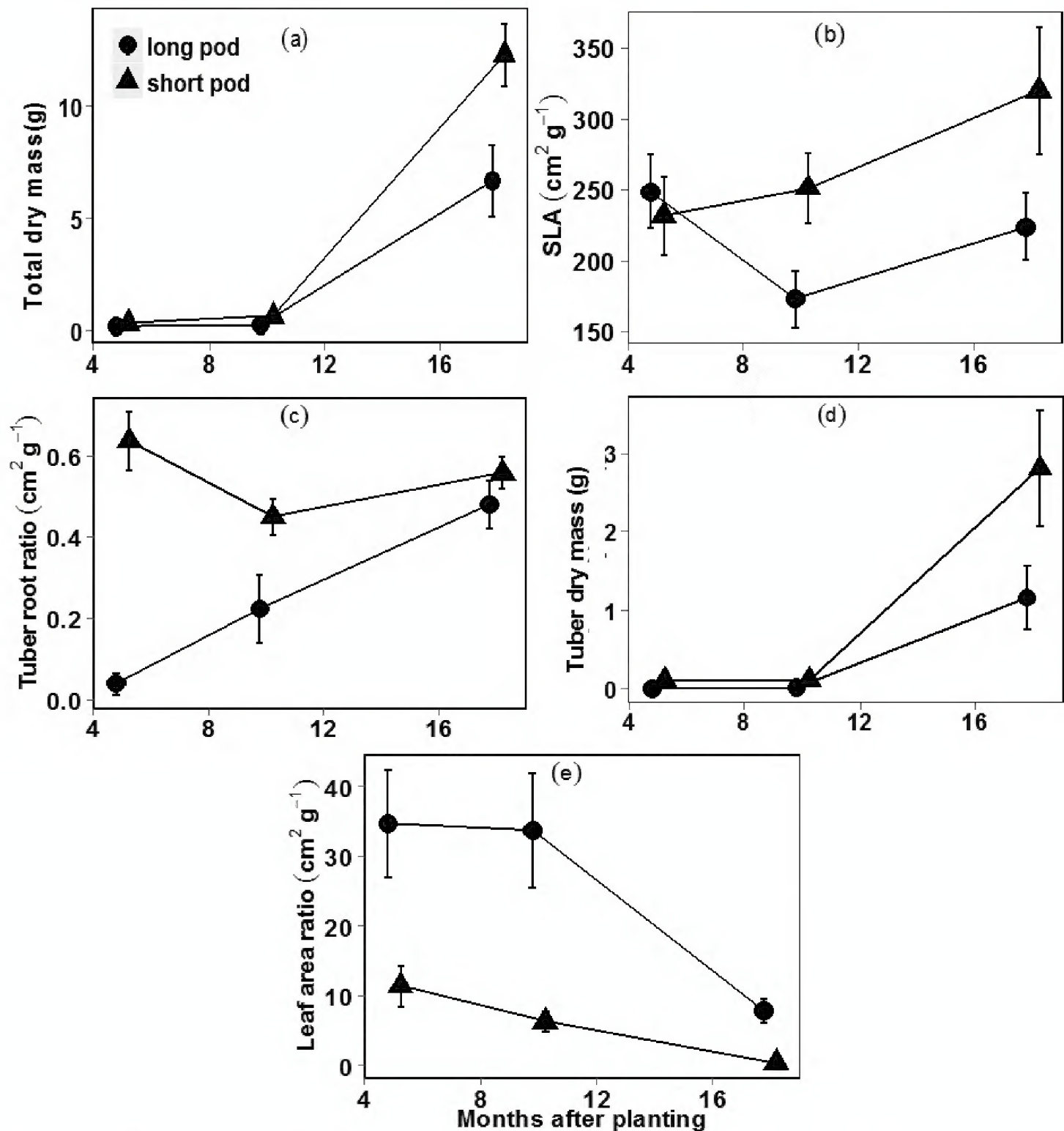


Figure 1. Total biomass production and allocation patterns ($\pm$ SE; $N = 7$) to tubers and leaves for long pod and short pod over time. **a** Total dry mass **b** Specific leaf area (SLA) **c** Tuber/root ratio **d** Tuber dry mass and **e** leaf area ratio. The legend in panel **a** applies to the rest of the panels.

roots and tubers differed significantly between LP and SP after 18 months of plant growth ($P < 0.0005$, 0.021 and 0.002 , respectively). SP allocated more biomass to tubers, shoots (leaves + stems) and roots than LP, especially after 18 months of growth (Fig. 1b).

LP appears to have allocated a significantly higher percentage of its biomass belowground at 5 months; while, SP invested significantly more biomass to tubers than LP at the same time (Table 1 and Fig. 1d). Belowground biomass ratio (BMR) in LP gradually decreased while it increased in SP between 10 and 18 months respectively. After 5 and 10 months of growth, the proportion of tuber to root ratio (TRR) was

Table 1. Mean ($\pm$ SE) growth traits calculated at 5, 10 and 18 months after planting for LP and SP. Different letters indicate significant differences among age groups and between the two forms of *Dolichandra unguis-cati*. Summary ANOVA refers to F- and P-values of a MANOVA model of growth traits using fixed effects of form and age of plants, and an interaction of form: age of plants; d.f = 5, 36. Within each row, representing means across the age of plants, means with the same subscripts are not significantly different at $\alpha \leq 0.05$ using a Tukey LSD multiple comparison procedure. “****” = $P \leq 0.0001$; “***” = $P \leq 0.001$; “**” = $P \leq 0.05$; n.s = not significant.

Traits	Age of plants in months						Summary ANOVA	
	5			10				
	LP	SP	LP	SP	LP	SP	F-ratio	Signif.
Aboveground dry mass (g)	0.099 _a ± 0.023	0.200 _a ± 0.021	0.201 _a ± 0.047	0.430 _a ± 0.081	4.460 _b ± 0.922	7.580 _c ± 0.677	6.968	*
Root dry mass (g)	0.097 _a ± 0.023	0.057 _{ab} ± 0.009	0.073 _{ab} ± 0.019	0.137 _{ab} ± 0.027	1.043 _b ± 0.328	1.903 _c ± 0.295	5.524	*
Root mass ratio (RMR)	0.512 _a ± 0.062	0.151 _b ± 0.018	0.245 _c ± 0.035	0.221 _c ± 0.043	0.151 _b ± 0.016	0.154 _b ± 0.015	17.990	***
Belowground dry mass (g)	0.101 _a ± 0.029	0.174 _a ± 0.034	0.089 _b ± 0.018	0.253 _c ± 0.030	2.211 _c ± 0.723	4.719 _d ± 1.019	5.440	*
Tuber dry mass (g)	0.004 _a ± 0.003	0.117 _b ± 0.028	0.016 _c ± 0.007	0.118 _b ± 0.024	1.169 _d ± 0.412	2.816 _d ± 0.745	4.923	*
Tuber mass ratio (TMR)	0.020 _a ± 0.015	0.303 _b ± 0.053	0.071 _a ± 0.029	0.170 _c ± 0.020	0.148 _c ± 0.026	0.210 _d ± 0.038	9.163	**
Total dry mass (g)	0.200 _a ± 0.039	0.374 _a ± 0.034	0.290 _a ± 0.061	0.683 _b ± 0.116	6.671 _c ± 1.591	12.299 _d ± 1.391	7.455	**
Shoot/root ratio (SRR)	1.100 _a ± 0.270	4.556 _b ± 1.439	3.367 _c ± 0.726	3.540 _c ± 0.738	5.023 _d ± 0.615	4.543 _d ± 0.762	4.990	*
Tuber/root ratio (TRR)	0.040 _a ± 0.026	0.637 _{bd} ± 0.073	0.225 _b ± 0.085	0.451 _{bd} ± 0.044	0.481 _{bc} ± 0.060	0.558 _{cd} ± 0.039	17.189	***
Number of tubers	0.286 _a ± 0.184	1.571 _a ± 0.297	0.858 _a ± 0.261	1.286 _a ± 0.184	2.000 _a ± 0.309	5.143 _b ± 1.299	3.063	<i>n.s</i>
Tuber fresh mass (g)	0.009 _{ab} ± 0.006	0.399 _{ab} ± 0.091	0.075 _{ab} ± 0.030	0.541 _{ab} ± 0.107	4.597 _b ± 1.221	11.866 _c ± 2.709	7.630	**
Basal stem diameter (mm)	1.129 _a ± 0.083	1.283 _a ± 0.063	1.236 _a ± 0.062	1.371 _a ± 0.084	3.660 _b ± 0.234	3.236 _b ± 0.285	2.080	<i>n.s</i>
Stem length (cm)	7.143 _a ± 0.969	16.428 _{bc} ± 3.176	7.329 _a ± 0.997	31.958 _{ac} ± 3.755	99.786 _c ± 35.862	326.500 _d ± 38.305	20.430	***
Number of branches	0.000 _a ± 0.000	0.143 _a ± 0.143	0.143 _a ± 0.143	0.429 _a ± 0.202	2.143 _b ± 0.340	3.857 _c ± 0.404	7.837	**
Apical dominance index	N/A	N/A	N/A	N/A	1.1471 _a ± 0.436	6.461 _b ± 3.883	3.191	<i>n.s</i>
Leaf area (cm ²)	6.074 _{ac} ± 1.254	4.100 _{ac} ± 0.954	7.234 _{ac} ± 0.697	4.571 _{ac} ± 1.356	39.747 _b ± 3.194	5.288 _c ± 0.922	60.977	***
Leaf fresh mass (g)	0.086 _{ac} ± 0.018	0.062 _{ac} ± 0.013	0.116 _{ac} ± 0.014	0.067 _{ac} ± 0.021	0.562 _b ± 0.054	0.076 _c ± 0.015	55.677	***
Leaf dry mass (g)	0.027 _a ± 0.006	0.019 _a ± 0.003	0.052 _{ac} ± 0.008	0.020 _{ac} ± 0.007	0.192 _b ± 0.029	0.022 _c ± 0.005	39.144	***
Specific leaf area	248.93 _a ± 26.260	231.901 _a ± 27.795	173.174 _{ab} ± 20.3	251.3 _a ± 24.819	224.211 _a ± 23.352	320.035 _{ab} ± 45.317	3.180	<i>n.s</i>
Leaf matter per area	0.004 _a ± 0.0003	0.005 _a ± 0.001	0.008 _{ab} ± 0.002	0.005 _a ± 0.0002	0.005 _a ± 0.001	0.004 _a ± 0.001	0.434	<i>n.s</i>
Leaf water content (g)	0.059 _{ac} ± 0.012	0.043 _{ac} ± 0.011	0.064 _{ac} ± 0.014	0.047 _{ac} ± 0.014	0.370 _b ± 0.030	0.054 _c ± 0.011	52.280	***
Leaf dry matter content (mg g ⁻¹)	32.871 _a ± 4.009	31.619 _a ± 2.083	51.44 _a ± 14.085	31.153 _a ± 1.317	33.377 _a ± 2.136	27.057 _a ± 2.368	0.037	<i>n.s</i>
Shoot mass ratio	0.468 _a ± 0.061	0.546 _{ab} ± 0.056	0.684 _{ab} ± 0.031	0.609 _{ab} ± 0.050	0.701 _b ± 0.027	0.636 _b ± 0.046	1.778	<i>n.s</i>

significantly higher for SP than LP, but after 18 months TRR values were similar (Fig. 1c). There was no significant difference in the shoot mass ratio (SMR) between the two forms (Table 1); however the leaf area ratio (LAR) for LP was significantly higher than that of SP over time (Fig. 1e). Specific leaf area (SLA) did not differ significantly at 5 months but differed significantly after this age, with SP having a higher SLA than LP. Leaf dry matter content (LDMC) or leaf area matter (LMA) was not significantly different between the two forms, except at 10 months when LP showed significantly higher LDMC than SP (Fig. 1 and Table 1).

Growth parameters

Except for BSD, other growth related traits such as number and size of tubers, length of stems, and number of branches differed significantly between 10th and 18th month old LP and SP (Fig. 2a, b, c, d). ADI, an indicator of branching architecture was significantly different only after 18 months (Table 1), but could not be calculated for 5 and 10 months due to lack of branching in LP and an insignificant number of branches for SP (Fig. 2b).

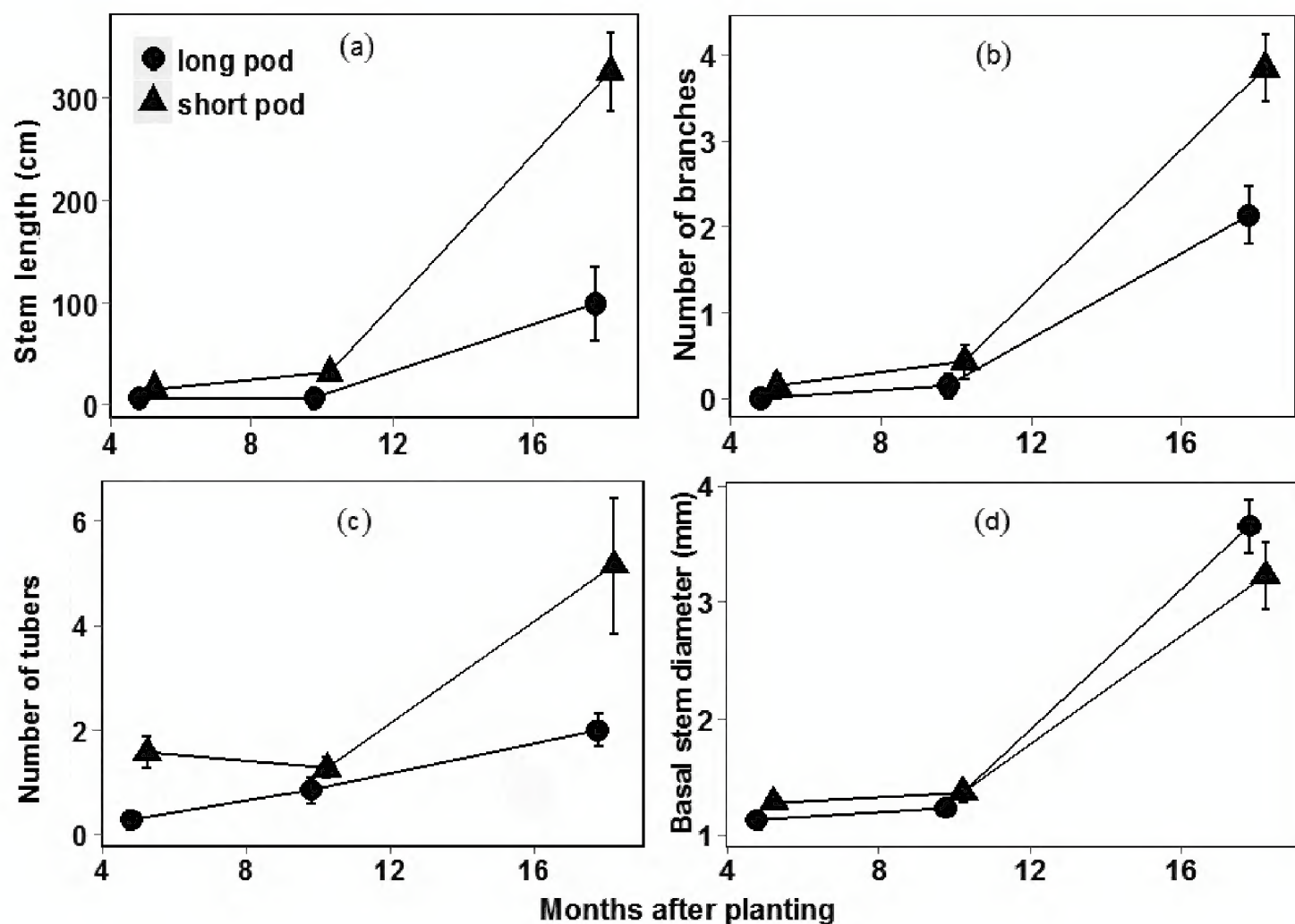


Figure 2. The pattern of resource allocation of LP and SP plants of varying ages in months, (mean $\pm$ SE, N=7). **a** Maximum stem length (cm) **b** Number of branches **c** Number of tubers **d** Basal stem diameter – (BSD) (mm).

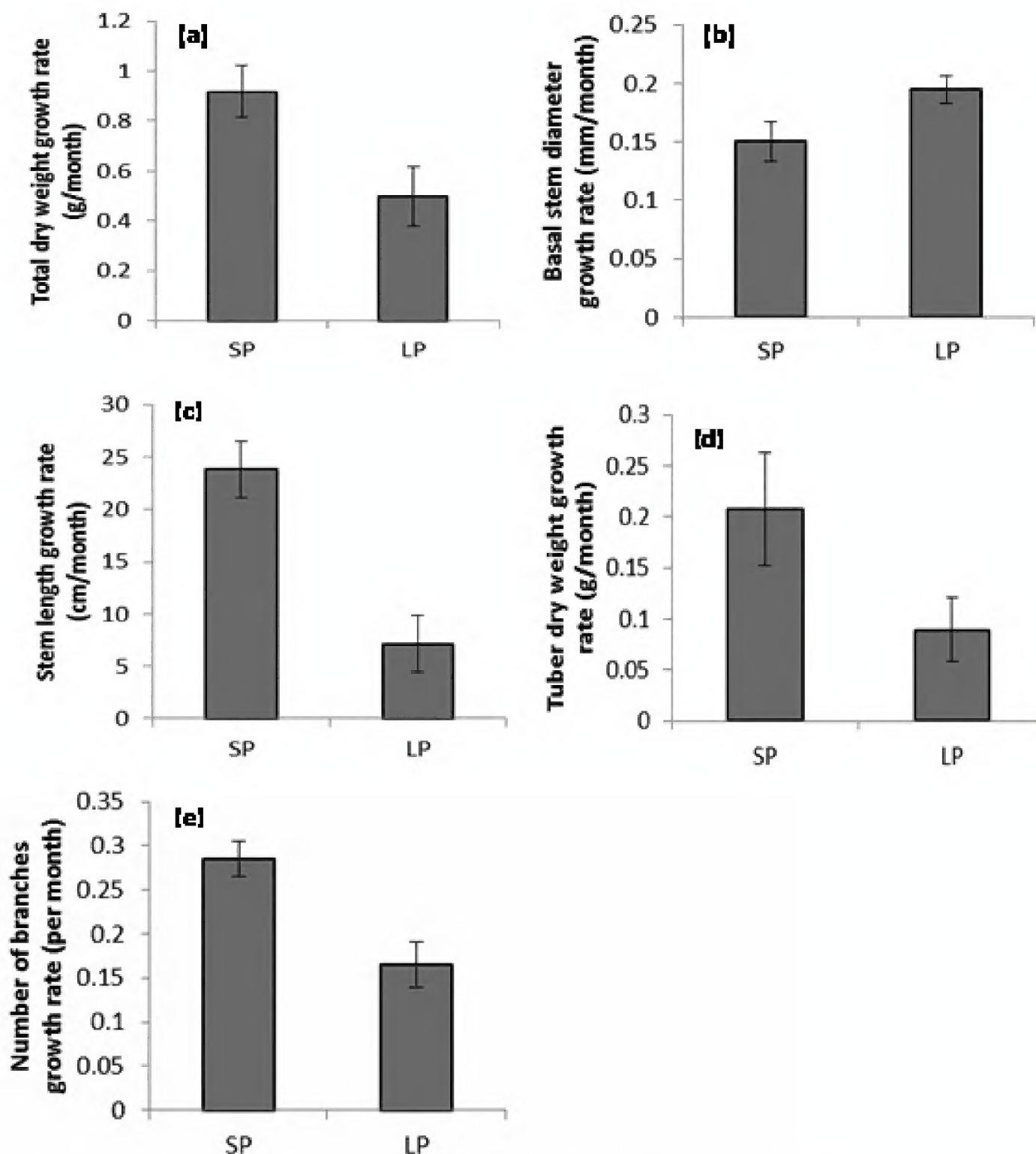


Figure 3. Comparison of absolute change of variables between long pod (LP) and short pod (SP) plants in the glasshouse (mean $\pm$ SE, $N = 7$) calculated between 10 and 18 months: **a** change in total dry weight per month **b** change in basal stem diameter (BSD) per month **c** change in stem length per month **d** change in tuber dry weight per month and **e** increase in the number of branches per month.

Estimates of growth rate such as change in total biomass ($F_{1,39} = 47.03$, $p < 0.001$), stem length ($F_{1,39} = 47.05$, $p < 0.0001$) tuber dry weight ($F_{1,39} = 19.43$, $p < 0.005$) and number of branches ($F_{1,39} = 61.49$, $p < 0.0001$) differed significantly between the two forms over time (Fig. 3a, c, d, e). SP showed a higher rate of change in total biomass, stem length and tuber biomass than LP (Table 1). Change in BSD did not differ significantly between the two varieties over time (Fig. 3b).

Overall, the observed differences between LP and SP can be summarized by the PCA graphical representation (Fig. 4), where traits of both forms largely overlap at 5

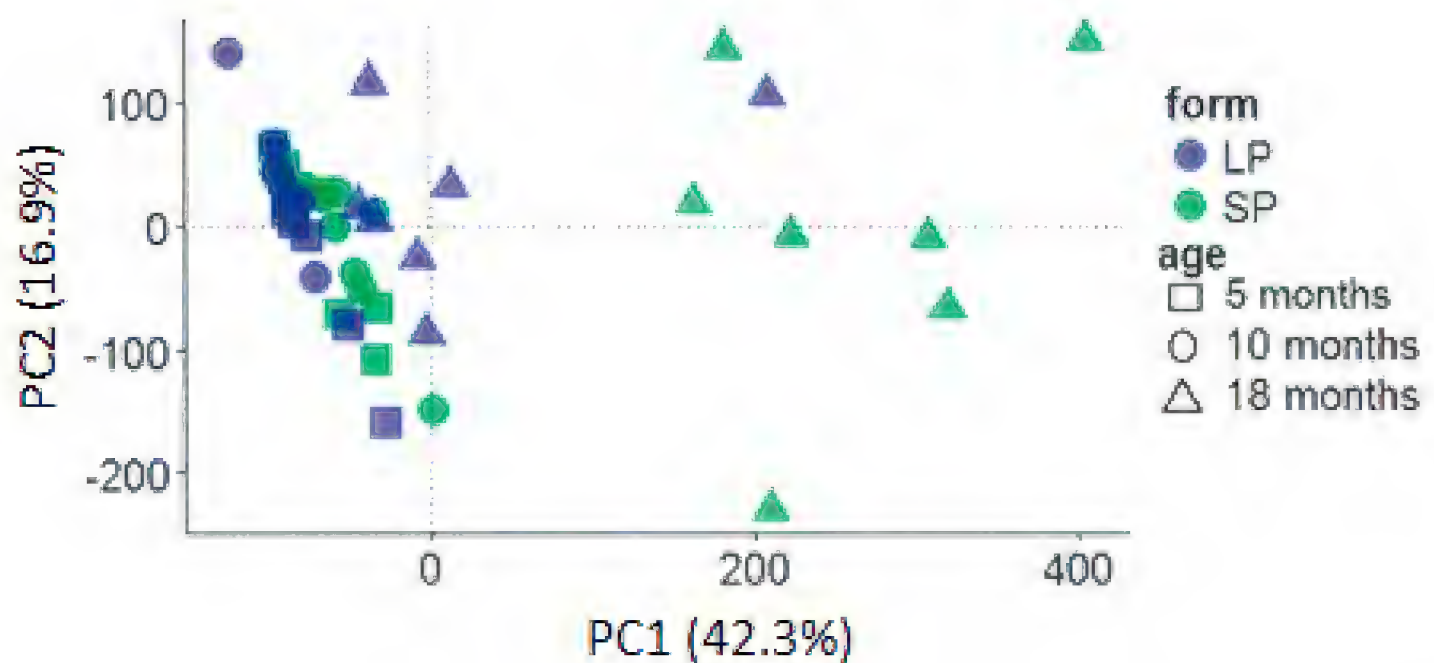


Figure 4. Graphical representation of the first and second PCA axes of different plant traits analysed for form (LP vs SP) and age of the plants (5, 10 and 18 months).

and 10 months but SP can be clearly distinguished at 18 months. PC1 (the principal axis of variation) together with PC2 explained about 60% of the total variation of the data (see Fig. 4 and Table 2). Some of the traits that were positively associated with PC1 were total dry mass, tuber dry mass, number of branches, stem length and basal stem diameter. These traits are indicators of relative growth of a plant, in terms of mass and height. PC2 was positively correlated with apical dominance index, root mass ratio and number of tubers while negatively associated with shoot/root ratio, shoot mass ratio and basal stem diameter (Table 2).

Discussion

The SP form, which is more widely distributed within eastern Australia, showed faster growing strategies. Higher values of RGR, stem length, number of tubers, and SLA are often indicators of successful colonizers (Gallagher et al. 2015; Holaday et al. 2015). Higher values of RGR normally correlate with high values of leaf area ratio (LAR) and SLA (Garcia-Serrano et al. 2005). These results are in accordance with the predictions of the ‘leaf economic spectrum’ (LES) hypothesis (Wright et al. 2004), which suggests a fundamental trade-off in the traits held by fast- and slow-growing plant species. According to the LES theory, where a species can be found within the spectrum is associated with strategies for resource capture and use. At one extreme are faster growing and highly productive species while on the other end slower growing and more conservative species occupy (Holaday et al. 2015).

Recent evidence, however, suggests the same carbon assimilation strategies are used by invasive and non-invasive plants (Leishman et al. 2010), but invasive plants

Table 2. Principal component loadings of the data set, eigenvalues and their contributions to the correlations, showing only the first four components.

Traits	PC1	PC2	PC3	PC4
Total dry mass (g)	1.037	0.211	0.184	-0.086
Shoot dry mass (g)	1.021	0.089	0.134	-0.061
Root dry mass (g)	0.994	0.272	0.292	-0.099
Tuber dry mass (g)	0.942	0.424	0.206	-0.124
Shoot mass ratio	0.294	-0.749	-0.492	-0.243
Root mass ratio	-0.632	0.417	0.704	0.222
Tuber mass ratio	0.465	0.334	-0.328	-0.002
Shoot/root ratio	0.409	-0.471	-0.671	-0.095
Tuber/root ratio	0.647	0.042	-0.548	0.001
Number of tubers	0.838	0.460	-0.037	-0.229
Basal stem diameter (mm)	0.927	-0.266	0.232	0.129
Stem height (cm)	0.844	0.217	-0.083	-0.114
Number of branches	0.974	0.116	0.035	-0.040
Apical dominance index	0.588	0.528	0.109	-0.245
Leaf area (cm ²)	0.517	-0.757	0.457	0.313
Leaf area ratio (cm ² g ⁻¹)	-0.637	-0.128	0.268	-0.173
Specific leaf area (cm ² g ⁻¹)	0.285	0.354	-0.402	0.569
LDMC (mg g ⁻¹)	-0.275	-0.232	0.422	-0.878
Importance of components				
Eigen values	11.811	4.729	3.523	2.220
Proportion explained	0.422	0.169	0.126	0.079
Cumulative proportion	0.422	0.591	0.717	0.796

have a tendency to cluster towards the ‘high return on investment’ end of the world wide leaf economic spectrum (Funk et al. 2013). Although SP seems to lean towards this end of the spectrum for some traits at 18 months, there were significant overlaps with LP earlier in the plants’ growth. Most studies simply consider ‘adult’ traits (e.g. Bachmann et al. 2012; Burns 2006; Hulshof and Swenson 2010), so we know very little about younger plants (but see Luo et al. 2015). In this study, there is evidence that trait differences are minimal up to 10 months old, but after this age our results suggest that they begin to differ between LP and SP. In our study, PCA shows that the two forms are different at 18 months with the variation mostly explained by growth related traits (PC1), followed by difference in how biomass is allocated below- and above-ground (PC2).

Our results also seem to contradict findings by Taylor and Dhileepan (2012) who observed that LP had higher growth rates than SP in the field. These differences could be attributable to environmental (Evans and Hughes 1961) and growing conditions (field vs glasshouse) (Limpens et al. 2012). Moreover, whilst we generated experimental plants from seeds (seedlings) in our experiments, Taylor and Dhileepan (2012) used plants grown from tuberslings. Also, in the current experiment, plants were not supported while in Taylor and Dhileepan (2012) they were supported with trellises. Our study could also be limited by lack of additional nutrients in the commercial

potting mix, although all individuals in the experiment were treated the same and therefore growth and response is comparable.

Although SP had slightly higher values of SLA, it had lower values of LAR when compared to LP. Because LAR is a measure of the leafiness of a plant (Radford 1967), our results imply that although LP might be leafier, SP invests more biomass to branches and stems, which could be a benefit for growing taller and spreading wider. Higher SLA has been positively correlated with high RGR and more rapid turnover of leaf material (Grotkopp et al. 2002). By rapid growth and quick tissue turnover, plants ensure that they outcompete others for limited resources (Gallagher et al. 2015). High growth rates by more successful species are particularly important in the seedling stage of a plant's life history (Grotkopp et al. 2002). Developing more branching is highly advantageous for vines as it is a way to increase LAR and LMR for maximum harvesting of light in order to optimise photosynthesis. Our results partly corroborate this hypothesis as we found that SP displayed higher values for SLA and LMR (but not for LAR) than LP. By developing more branches than LP (indicated by higher ADI values), SP can effectively out-compete other competitors in the environment for limiting resources.

Transformer plants such as vines like *D. unguis-cati*, thrive in growing vertically and spreading horizontally to monopolise light environments (Heckel 2004). The negative impacts of this group of plants lie in their ability to smother host tree canopies that they use as supporting structures (Harris and Gallagher 2011; Harris et al. 2007; Zhang et al. 2004). *Dolichandra unguis-cati* forms thick mats of intertwining creeping stems and branches on forest floors (Osunkoya et al. 2009). Thus, ensuring rapid elongation of stems and a higher branching architecture may be central to the successful colonization of empty habitats by SP. This pattern of growth reduces light availability to low lying vegetation and may prevent recruitment of native plants (Downey and Turnbull 2007; Schnitzer and Bongers 2002; Zhang et al. 2004).

This study shows that SP develops subterranean tubers early in its development while LP seems to delay tuber development. Tubers are used as a sink or storage organs for moisture and photo-assimilates and they may also regenerate producing new plants (Janeček and Klimešová 2014; Orthen 2001; Schubert and Feuerle 1997). Apart from seed germination (Buru et al. 2014; Vivian-Smith and Panetta 2004), *D. unguis-cati* propagates vegetatively through tubers (Downey and Turnbull 2007; Osunkoya et al. 2009). Horizontal stems and branches trailing along the ground develop roots at nodes, which in turn develop tubers. If the new plants regenerating at the nodal tubers are severed from the mother plant, they grow independently as genets. This study shows that SP develops significantly more tubers per plant than LP, which could be a clonal survival strategy to increase its competitiveness. Clonal growth of a species may enhance its invasion success by way of rapid formation of monocultures (Aguilera et al. 2010; Pyšek and Richardson 2007). Liu et al. (2006) found a positive relationship between clonality and invasiveness. They found that more than 66% of the most invasive plants they studied in China were clonal. Resource storage by clonal plants function as a back-up measure in case of adverse alterations in the growth conditions of the plant (Suzuki and Stuefer 1999). Tubers can also remain dormant for extended periods belowground as a stress tolerance strategy (Orthen 2001).

Conclusion

Previous studies have shown SP to exhibit more rapid and higher germination rates than LP at various temperatures (Buru et al. 2014) and a higher frequency of polyembryony than LP (Buru et al. 2016). Seeds of the two forms do not differ in their average mass (Shortus and Dhileepan 2011). This study has shown that SP displayed superior values of traits known to be associated with successful invaders (Chun et al. 2007; van Kleunen et al. 2015). Therefore it may be safe to assume that were the two forms to be introduced into novel environments at the same time, SP would likely be more successful in colonizing the habitats than LP (Gallagher et al. 2015; Godoy et al. 2012; Kolar and Lodge 2001; Pyšek and Richardson 2007; van Kleunen et al. 2010). Thus, our results partly explain why SP seems to be abundant in Australia, although LP is postulated to also have a potential to become widespread if not carefully managed (see Taylor and Dhileepan 2012).

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